Products of Random Matrices or 'Why do Biennials Live Longer than Two Years?'

J.B.T.M. Roerdink
Centre for Mathematics and Computer Science
P.O. Box 4079, 1009 AB Amsterdam, The Netherlands

We study a population model with two age classes which describes the growth of biennial plants in a randomly fluctuating environment. A fraction of the oldest age class delays its flowering each year. Using the theory of random matrix products we show that delay of flowering increases the growthrate of the population. We investigate the dependence of the optimal flowering fraction on the model parameters.

Note. This paper is dedicated to Prof. H.A. Lauwerier on the occasion of his 65th birthday.

1. Introduction

Strictly biennial plants lead a vegetative existence in the first year, flower in the second year and then die. In natural populations of 'biennials' often a large fraction of the plants delays its flowering past the second year: the non-reproductive period of a lineage may span 2-5 years. This is surprising because classical life-history theory predicts that a biennial has to produce four times as many seeds as a perennial and twice as many seeds as an annual plant to attain the same rate of increase. This conclusion was reached by assuming a deterministic (nonchanging) environment.

This picture changes completely when the population grows in a randomly fluctuating environment. Simulation studies by Klinkhamer & De Jong [1] indicated that some delay of flowering is profitable if the per capita reproductive success varies strongly over the years. These authors used the following discrete-time model pertaining to the case of density-independent population growth:

$$\begin{pmatrix} N_{1,t+1} \\ N_{2,t+1} \end{pmatrix} = \begin{pmatrix} 0 & f\varphi_t \\ s & (1-f)s \end{pmatrix} \begin{pmatrix} N_{1,t} \\ N_{2,t} \end{pmatrix} \quad t = 0,1,2,..., \tag{1.1}$$

where t is a time just before flowering, and

$N_{1,t}$ the number of individuals which are one year old at time t;
$N_{2,t}$ the number of individuals older than one year at time t;
s survival rate of individuals older than one year, $0 \leqslant s \leqslant 1$;
f fraction of individuals older than one year that flowers in a given year, $0 \leqslant f \leqslant 1$;

φ_t fluctuating number of offspring per flowering plant after one year, $\varphi_t \geqslant 0$.

We assume that $\{\varphi_t\}$ is a sequence of independent, identically-distributed (i.i.d.) random variables, where each φ_t has a two-parameter gamma distribution with density given by

$$g(\varphi) = \{k^a/\Gamma(a)\}\varphi^{a-1}e^{-k\varphi}, \quad a>0, \quad k>0, \tag{1.2}$$

with $\Gamma(a)$ the gamma function. Mean and variance of this distribution are

$$\bar{\varphi} := \mathbb{E}(\varphi) = a/k; \quad \bar{\bar{\varphi}} := \mathrm{Var}(\varphi) = a/k^2, \tag{1.3}$$

where $\mathbb{E}$ denotes the mathematical expectation operator.

The long-run properties of the solution of (1.1) depend on the behaviour of the random matrix products $M_t M_{t-1} \cdots M_0$, where M_t is the two-by-two matrix in (1.1). Below we give an informal presentation of the results which have been obtained for this model in [2] by using the theory of products of random matrices (for the latter see e.g. [3,4]). In particular we will discuss the existence of an optimal flowering fraction, f_{opt}, for our model and discuss how the value of f_{opt} depends on the model parameters $s, \bar{\varphi}$ and $\bar{\bar{\varphi}}$. We do not go into the question as to how the delayed flowering is brought about in natural populations. For a more extensive discussion of this point and other biologically relevant questions we refer to [5].

2. Average behaviour is not typical behaviour

The aim of this paragraph is to define the concept of 'optimal flowering fraction' and to bring out the difference between deterministic and stochastic environments with regard to the proper definition of this concept.

First we will look at the *deterministic* case. So let us assume that φ_t in (1.1) has a constant value $\bar{\varphi}$ (which will later be identified with the average value of φ_t in the stochastic case). We define the optimal flowering fraction f_{opt} in this case as the value of f for which the total population $N_t := N_{1,t} + N_{2,t}$ has a maximal growthrate μ_0, defined by

$$\mu_0 := \lim_{t\to\infty} \frac{1}{t} \ln N_t. \tag{2.1}$$

It is easy to see that μ_0 is equal to $\ln \lambda_0(f)$, where λ_0 is the maximal eigenvalue of the matrix M_t with $\varphi_t = \bar{\varphi}$; λ_0 is given by

$$\lambda_0(f) = \tfrac{1}{2}[s(1-f) + \{s^2(1-f)^2 + 4f\bar{\varphi}s\}^{1/2}]. \tag{2.2}$$

If we assume that without delayed flowering the population is *increasing*, i.e. $\lambda_0(1) = (\bar{\varphi}s)^{1/2} > 1$, then delayed flowering is not profitable since λ_0 (or μ_0) is an increasing function of f for $\bar{\varphi}s > 1$ (in fact for $\bar{\varphi} > s$). As an example we have plotted μ_0 as a function of f for the parameter values $s = 0.9$, $\bar{\varphi} = 2$ in Figure 1 (broken line).

If we now turn to the case of a *random* environment our first difficulty is the choice of the optimality or 'fitness' criterion to be used in defining an optimal

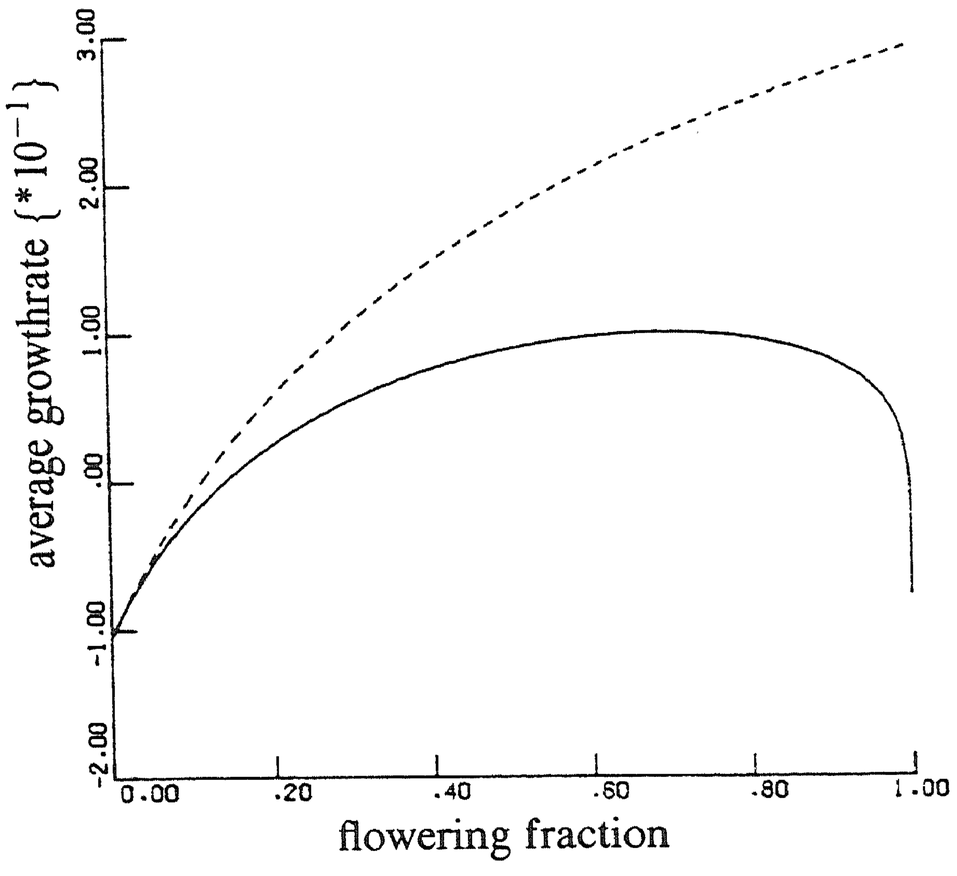

FIGURE 1. Geometric growthrate γ (solid line) and arithmetic growthrate μ_0 vs. the flowering fraction f; $s=0.9$; $\overline{\varphi}=2$, $\overline{\overline{\varphi}}=5$.

flowering fraction. There are at least two intuitively plausible ways to generalize the maximization of (2.1). First, we may maximize the growthrate of the average population, defined as

$$\mu = \lim_{t\to\infty} \frac{1}{t} \ln \mathbb{E}(N_t). \tag{2.3}$$

In fact, $\mu=\mu_0=\ln\lambda_0$ with λ_0 given by (2.2), where now $\overline{\varphi}$ is the average of φ_t. A second possibility is to consider the average growthrate (also called the upper Lyapunov exponent) defined by

$$\gamma = \lim_{t\to\infty} \frac{1}{t} \mathbb{E}(\ln N_t). \tag{2.4}$$

In general the arithmetic growthrate μ will be strictly larger than the geometric growthrate γ.

The theory of random matrix products tells us that a typical realization is characterized by γ, not by μ. More precisely, under some mild conditions (which are satisfied in our case),

$$\lim_{t\to\infty} \frac{1}{t} \ln N_t = \gamma \tag{2.5}$$

for almost all sequences of matrices $\{M_t\}$ and any initial value $N_0\neq 0$. Thus, although eventually each population growing according to (1.1) attains a growthrate γ, there are at each given time t, no matter how large, always

populations which have been growing at a much larger rate, due to a rare succession of years with favourable environmental conditions. It is because of these exceptional realizations that the average (2.3) differs from the typical growthrate γ. Also, it can be shown that a maximal geometric growthrate is the biologically appropriate 'fitness criterion': if in a population with geometric growthrate γ_0 a mutant occurs with growthrate γ_1, then the mutant will invade and eventually outnumber the original population if $\gamma_1 > \gamma_0$.

The analytical computation of γ is in general not a trivial matter. In fact there are only a few models for which γ has been explicitly determined, our model (1.1) being one of them. The calculation will be briefly sketched in the next paragraph.

3. The upper Lyapunov exponent γ

First we introduce the following notation.

$$x_t = (N_{1,t}, N_{2,t}), \tag{3.1}$$

$$|x_t| = N_t = N_{1,t} + N_{2,t}, \tag{3.2}$$

$$\bar{x}_t = x_t / |x_t|. \tag{3.3}$$

In biological terms: x_t is the population vector, $|x_t|$ the total population and $\bar{x}_t$ the 'age-structure'. So $\bar{x}_t$ is defined on the simplex

$$C = \{x \in \mathbb{R}^2 : x_1 \geqslant 0,\ x_2 \geqslant 0,\ x_1 + x_2 = 1\}. \tag{3.4}$$

Every time the iteration (1.1) is applied we get a new population vector x_t and corresponding age-structure $\bar{x}_t$, see Figure 2. The sequence $\{\bar{x}_t\}$ constitutes a Markov chain on the simplex C and the distribution of age-structures evolves towards a unique stationary probability measure $\nu(\bar{x})$, which is invariant with respect to the common distribution $\mu(M)$ of the matrices $\{M_t\}$.

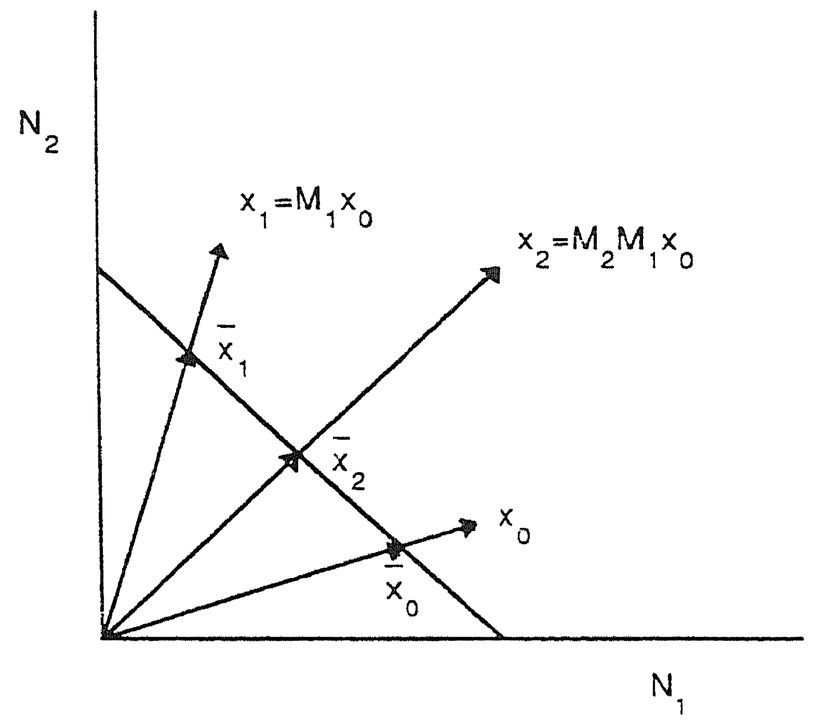

FIGURE 2. Iterates of the population vector x_t and the age-structure $\bar{x}_t$ under the action of (1.1).

In terms of the given measure μ and the (as yet unknown) measure ν the expression for the growthrate γ is,

$$\gamma = \int\int \ln|M\bar{x}|d\mu(M)d\nu(\bar{x}). \tag{3.5}$$

The problem is therefore to determine the stationary age-structure distribution ν. It is convenient to introduce the scaled variable

$$\tau_t = (1-f)^{-1}\{N_{1,t}/N_{2,t}\}, \tag{3.6}$$

so that (1.1) can be written as

$$\tau_{t+1} = \eta\varphi_t/(1+\tau_t) \tag{3.7}$$

where

$$\eta = f\{(1-f)^2 s\}^{-1}. \tag{3.8}$$

For the invariant measure expressed in the variable τ we write $\tilde{\nu}(\tau)$. The corresponding density (which exists) is denoted by $h(\tau)$. By using the invariance of $h(\tau)$ under the action of (3.7) one can derive the integral equation

$$h(\tau) = \int_0^\infty h(\tau')g\left[\frac{(\tau'+1)\tau}{\eta}\right]\left[\frac{\tau'+1}{\eta}\right]d\tau' \tag{3.9}$$

where $g(\cdot)$ is the gamma distribution (1.2). The solution is

$$h(\tau) = K^{-1}\tau^{a-1}(1+\tau)^{-a}e^{-z\tau} \tag{3.10}$$

where K is a normalization constant.

By using this result in (3.5) and performing some simplifications in the resulting formula one ends up with the following expression for $\gamma=\gamma(f)$,

$$\gamma(f) = \ln\{s(1-f)\} + \frac{\int_0^\infty \{\ln(1+\tau)\}\tau^{a-1}(1+\tau)^{-a}e^{-z\tau}d\tau}{\int_0^\infty \tau^{a-1}(1+\tau)^{-a}e^{-z\tau}d\tau}, \tag{3.11}$$

where

$$z = ks(1-f)^2/f. \tag{3.12}$$

The limiting values at the endpoints of the interval [0,1] are,

$$\gamma(0) = \ln s, \quad \gamma(1) = \tfrac{1}{2}\{\ln(s/k)+\psi(a)\} \tag{3.13}$$

where $\psi(a)=\frac{d}{da}\Gamma(a)$ is the digamma function. As a final remark we note that the second term in the right hand side of (3.11) can be expressed in terms of Kummer functions and derivatives thereof [2].

4. Maximizing the fitness

The biologically interesting question is now to see for which values of the flowering fraction f the geometric growthrate γ attains a maximum. If such a maximum occurs for a value $f_{opt}<1$ then delayed flowering is profitable.

First we calculate γ as a function of the flowering fraction f for the parameter values $s=0.9$, $\bar{\varphi}=2$, $\bar{\bar{\varphi}}=5$ (where $\bar{\varphi}$, $\bar{\bar{\varphi}}$ are the mean and variance of the offspring number φ_t), see the solid curve in Figure 1. The result is obtained by numerical evaluation of the integrals occurring in (3.11). We note the following:

(i) γ attains a maximum for a value $f_{opt}<1$: delayed flowering is profitable ('spreading of the risk')

(ii) $\gamma<\mu$ for $0<f\leqslant 1$. In fact $\mu(1)>0$, $\gamma(1)<0$, so if $f=1$ the population will almost surely go extinct whereas the average population increases indefinitely!

(iii) a very steep decrease of γ near $f=1$ is observed (in fact [2]: $\frac{d\gamma}{df}|_{f=1}=-\infty$): even a tiny amount of delayed flowering is advantageous. The precise amount is not very crucial, as can be seen from the small variation of γ in the region $0.5\lesssim f\lesssim 0.9$.

Of course the value of f_{opt} will depend on the parameters of the model, i.e. on s, a and k or, equivalently, on $s, \bar{\varphi}$ and $\bar{\bar{\varphi}}$. In Figure 3 we have plotted γ as a function of f for the values $s=0.3, 0.5, 0.7, 0.9$ with $\bar{\varphi}=2$, $\bar{\bar{\varphi}}=5$. The optimal fraction f_{opt} increases as s decreases. This is to be expected since a smaller survival probability has to be balanced by a larger amount of flowering.

In Figures 4 and 5 we show curves of γ versus f for various values of $\bar{\varphi}$ and $\bar{\bar{\varphi}}$ respectively, keeping the other parameters fixed. One observes that f_{opt} decreases as the average offspring number $\bar{\varphi}$ decreases or its variance $\bar{\bar{\varphi}}$ increases. Hence if the average reproductive success is low or varies strongly there is a strong environmental pressure on the population to delay its flowering.

Field studies of biennials suggest that the model (1.1) is certainly inadequate in many respects, see e.g. [5]. For example, no density dependence is assumed and there is no advantage of delayed flowering through increased probability of survival and increased seed production. Nevertheless, the prediction of the simple model (1.1) that f_{opt} is considerably smaller than unity for a wide range of parameters is in agreement with the fact that only very few species are strictly biennial.

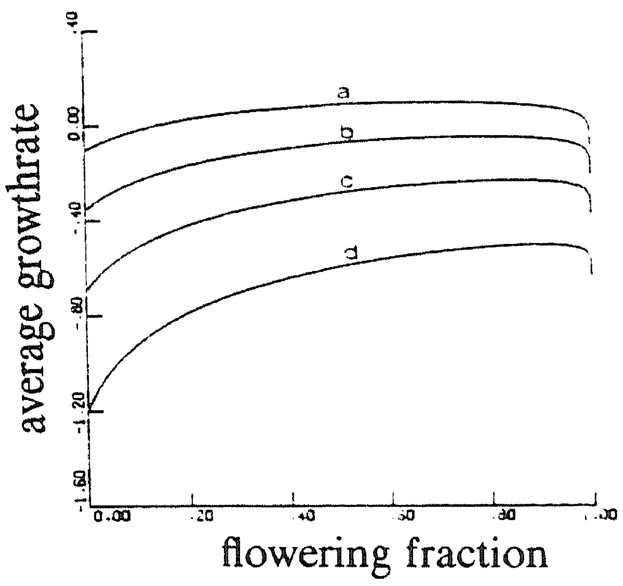

FIGURE 3. Geometric growthrate vs. the flowering fraction ($\bar{\varphi}=2$, $\bar{\bar{\varphi}}=5$); (a) $s=0.9$; (b) $s=0.7$; (c) $s=0.5$; (d) $s=0.3$.

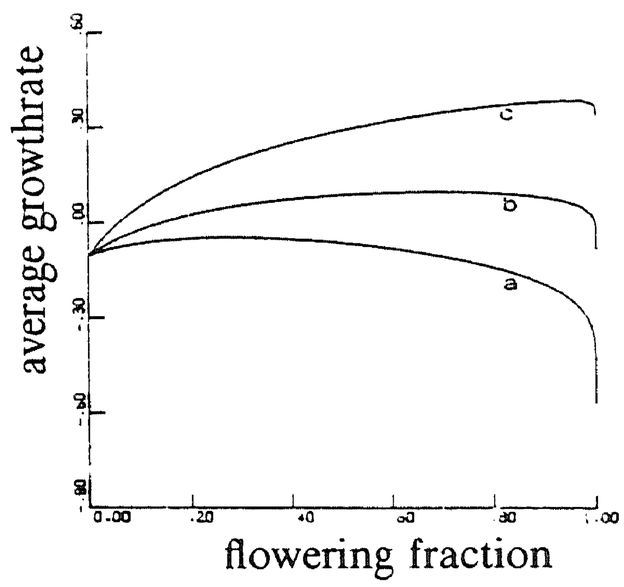

FIGURE 4. Geometric growthrate vs. the flowering fraction ($s=0.9$, $\bar{\bar{\varphi}}=5$); (a) $\bar{\varphi}=1$; (b) $\bar{\varphi}=2$; (c) $\bar{\varphi}=3$.

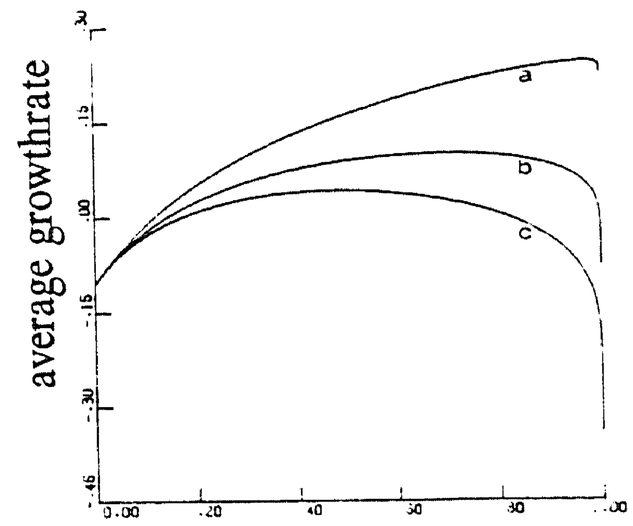

FIGURE 5. Geometric growthrate vs. the flowering fraction ($s=0.9$, $\bar{\varphi}=2$); (a) $\bar{\bar{\varphi}}=1$; (b) $\bar{\bar{\varphi}}=5$; (c) $\bar{\bar{\varphi}}=8$.

References

1. P.G.L. Klinkhamer, T.J. de Jong (1983). Is it profitable for biennials to live longer than two years? *Ecol. Modell. 20,* 223-232.
2. J.B.T.M. Roerdink (1988). The biennial life strategy in a random environment. *J. Math. Biol. 26,* 199-215, and Supplement (to appear).
3. J.E. Cohen, H. Kesten, C.M. Newman (eds.) (1986). *Random Matrices and their Applications,* A.M.S., Providence (Contemporary Mathematics, Vol. 50).
4. P. Bougeröl, J. Lacroix (1985). *Products of Random Matrices with Application to Schrödinger Operators,* Birkhäuser, Boston (Progress in Probability and Statistics, Vol. 8) Part A.
5. T.J. de Jong, P.G.L. Klinkhamer, S.A.H. Geritz and E. van der Meijden. Why biennials delay flowering: an optimization model and field data on Cirsium vulgare and Cynoglossum officinale. *Acta Botanica Neerlandica,* submitted.